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PREDICTING THE RESPONSE OF POPULATIONS TO ENVIRONMENTAL CHANGE¹

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Abstract. When subject to long-term directional environmental perturbations, changes in population densities depend on the positive and negative feedbacks operating through interactions within and among species in a community. This paper develops techniques to predict the long-term responses of population densities to environmental changes using data on short-term population fluctuations driven by short-term environmental variability. In addition to giving quantitative predictions, the techniques also reveal how different qualitative patterns of species interactions either buffer or accentuate population responses to environmental trends. All of the predictions are based on regression coefficients extracted from time series data, and they can therefore be applied with a minimum of mathematical and statistical gymnastics.

Key words: *community ecology; environmental change; population dynamics; species interactions; stochastic models.*

INTRODUCTION

One of the great challenges in ecology is to predict how environmental fluctuations change the abundances of species in a community (Kareiva et al. 1993). This challenge is particularly pressing in a world undergoing major anthropogenic environmental changes, such as lake acidification (Charles 1991), increasing levels of toxins in the air and water (Graedel and Crutzen 1990), and the possibility of anthropogenic global climate change (Schneider 1993). The difficulty in predicting the consequences of environmental changes is that changes in the abundance of a species depend not only on the direct effects of the environment on its survival and fecundity, but also the indirect effects of interactions with other species in the community (Connell 1961, Paine 1966, 1980, Davidson et al. 1984, Schindler 1990, Webster et al. 1992, Ives and Gilchrist 1993, Wootton 1994). Interactions with other species produce both positive and negative feedbacks that determine the ultimate response of population densities to environmental changes.

When discussing the response of populations to environmental changes, it is important to distinguish between short-term environmental fluctuations and long-term environmental trends. Short-term environmental fluctuations continuously buffet populations and produce the variability in population densities seen in many species (Strong 1986a, b). A large number of theoretical studies are devoted to short-term environmental fluctuations, asking what types of life history characteristics and community interactions act to buffer population densities against environmentally driven variability (e.g., May 1973, 1974, Leigh 1975, Rough-

garden 1975, Turelli 1977, 1978, Turelli and Gillespie 1980, Nisbet and Gurney 1982, Ives 1995). In contrast to short-term environmental fluctuations, long-term environmental trends may occur slowly enough for population densities to track. For long-term environmental trends, interactions among species are particularly important in determining how population densities change, since slow environmental changes allow time for indirect interactions among species to have strong effects (Levins 1975, Levine 1976, Yodzis 1989).

The conceptual differences between short- and long-term environmental changes are illustrated by the discussion in Bender et al. (1984) of two different types of experiments, PULSE and PRESS experiments. In PULSE experiments, interactions among species are measured by imposing a sudden shock to a community such as greatly increasing or decreasing the density of one species. These experiments may be analyzed to determine how interactions among species affect the rate at which densities return to their pre-shock levels. Short-term environmental fluctuations operate in a similar fashion, although shocks to the system occur frequently rather than just once. In PRESS experiments, a perturbation is applied by shifting some structural feature of the community to a different level, for example by elevating food availability for some species in a community. In this case, interactions among species are seen in the re-establishment of new population abundances, rather than in the return (or non-return) of population densities to former values following a shock in a PULSE experiment. Long-term environmental trends operate in the same fashion as PRESS experiments if population densities can track slow environmental changes.

This paper has two goals. The first is to develop techniques to predict how population abundances will change in response to long-term environmental trends.

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These techniques have the same mathematical structure as "loop analysis" (Levins 1975, Lane 1986, Yodzis 1989) in that they explicitly account for the interactions among species, incorporating both positive and negative feedbacks in the community. Changes in mean population abundances in response to environmental trends are predicted by analyzing the naturally occurring variability in population densities before the onset of the environmental trend. Thus, the objective is to predict the long-term (PRESS) changes in population densities in response to environmental trends from data on the short-term (PULSE) population responses to short-term environmental fluctuations.

The second goal of the paper is to partition out the different factors driving changes in mean population densities in response to environmental trends. The analysis shows that the response of the mean population density of a particular species to environmental trends depends on four factors: (1) the overall magnitude of the effect of the environmental change on all of the species in a community; (2) the pattern of how the environmental change affects different species within the community; (3) the overall strength of interaction that the particular species exerts on other species in the community; and (4) the pattern of interaction of the particular species with other species in the community. The first two of these factors are characteristics of the specific environmental stressor under investigation, while the third and fourth factors are properties of the biotic interactions within the community independent of the specific environmental stressor. Identifying which characteristics are specific to a particular environmental stressor and which are not has the pragmatic benefit of simplifying the study of multiple environmental stressors in the same community. Although the main focus in this paper is the response of populations to a single environmental stressor, natural communities are often subject to numerous stressors, and to examine each stressor independently would be an overwhelming task. Since the biotic factors 3 and 4 are independent of particular environmental stressors, this information can be shared among investigations of different environmental stressors.

This paper is divided into two parts. The first gives analyses of the response of a single species to environmental trends. Although these analyses are unrealistic in the sense that no species exists in isolation from all other species, they provide a useful starting point to develop the multispecies techniques. The second part of the paper analyzes multispecies communities. In addition to focusing on the changes in population density of a particular species, I also analyze how pairs of species will likely change in density with respect to each other. For example, if two species have similar functional roles in a community, will changes in the mean density of one species be compensated by opposite changes in the mean density of the other (Vitousek 1990, Frost et al. 1994)? In both the single and

multispecies sections I apply the prediction techniques to numerical examples. The object of these examples is to illustrate possible patterns in the response of species to environmental trends and to demonstrate the prediction techniques, rather than to do a thorough numerical analysis of the precision of the techniques.

SINGLE-SPECIES DATA

The general form of the data to be analyzed in this section is summarized by the equation

$$n(t + 1) = f[u(t), n(t), \omega(t)]. \quad (1)$$

Here, $n(t)$ is the population density of the species at time t , and $u(t)$ is the environmental stressor that undergoes a directional change in the mean. For example, for the case of lake acidification, $u(t)$ will be pH, and for global climate change, $u(t)$ might be mean June temperature or the number of frost-free days in a year. The parameter $\omega(t)$ represents environmental variability that does not undergo a directional change. The population growth rate $f[u(t), n(t), \omega(t)]$ depends on the population size, the environmental stressor that undergoes a directional change, and background environmental variability. Both $u(t)$ and $\omega(t)$ are random variables, characterized by a mean, variance, and other statistical moments.

Eq. 1 specifies several biological assumptions about the single-species data. First, environmental variability affects the population from one sample, t , to the next, $t + 1$. Many environmental factors will operate over a shorter time step than the population sampling. For example, an insect with a generation time of a year might be sampled only annually, while a cold snap in April during a vulnerable insect stage may cause high mortality in a single day. Even though an environmental stressor may act only over a short time, it may nonetheless affect changes in population densities between samples. The data described by Eq. 1 include any type of environmental variability that affects changes in density from one sample to the next. Second, Eq. 1 assumes that there is only a single environmental stressor that undergoes a long-term directional trend. For many types of environmental changes, a variety of environmental factors will be affected. For example, anthropogenic climate change is predicted to affect both temperature and precipitation (Schneider 1993). In addition, temperature itself cannot be considered a single variable if rising temperatures at one time of year have different effects on population dynamics than similar changes at another time of year. For simplicity of presentation, only the effects of a single environmental parameter are analyzed here, although multiple factors can be encapsulated into $u(t)$ by letting it denote some aggregate measure of the environment. Third, there is no population age structure or delayed effects of density dependence in the model (Turchin 1990, Murdoch 1993). Techniques for analyzing data with age structure and delayed density dependence will be sim-

ilar to those developed for multispecies interactions (Royama 1981, Turchin and Taylor 1992), although I do not develop these techniques here.

Despite these biological restrictions, the data can exhibit complicated patterns. The relationship between the population growth rate, $f[u(t), n(t), \omega(t)]$, and population density $n(t)$ and the environmental terms $u(t)$ and $\omega(t)$ may be nonlinear, and there may be interactions among these terms. Furthermore, the environmental terms $u(t)$ and $\omega(t)$ may be serially autocorrelated, as will be the case if multiple samples are taken each year and there are seasonal fluctuations in the environmental stressors. Since population densities depend on $u(t)$, autocorrelation in successive values of $u(t)$ will produce correlation between $n(t)$ and $u(t)$. Thus, Eq. 1 can describe complicated nonlinear population dynamics with complicated correlations among stochastic variables.

Simulated single-species example

Before developing the prediction techniques for single-species data, I will first give a simulated example to illustrate what types of patterns may arise in response to long-term environmental trends. After I develop the prediction techniques, I will apply them to this example.

Consider the stochastic version of the Ricker equation (May 1981):

$$n(t+1) = n(t) e^{\mu + u(t) + \omega(t) - rn(t)}. \quad (2)$$

The parameter r measures the strength of density dependence, with larger values implying a greater decrease in the per capita population growth rate with increasing density. The parameter μ scales the density-independent component of the per capita population growth rate. The random variable $u(t)$ produces variability in the density-independent population growth rate and is assumed to follow a normal distribution. Environmental variability other than $u(t)$ is included in the random variable $\omega(t)$, which is also distributed according to a normal distribution. Neither of the environmental random variables is autocorrelated; this simplifies the numerical analysis. In this example, the environmental stressor $u(t)$ appears as an exponent. Therefore, a log transform of the model makes $u(t)$ a linear term. Although this might appear a special case, suitable transforms may often be applied to real data sets to make population growth rates depend linearly on an environmental stressor. This will be true whenever the population growth rate is a monotonic function of the environmental stressor.

Eq. 2 is illustrated in Fig. 1, which shows a graph of $n(t+1)$ vs. $n(t)$ in the absence of environmental stochasticity. Greater values of r correspond to increased density dependence. For $r < 1$, the dynamics for population densities around the deterministic equilibrium are monotonic, while for $r > 1$, dynamics around equilibrium are overcompensating. The values

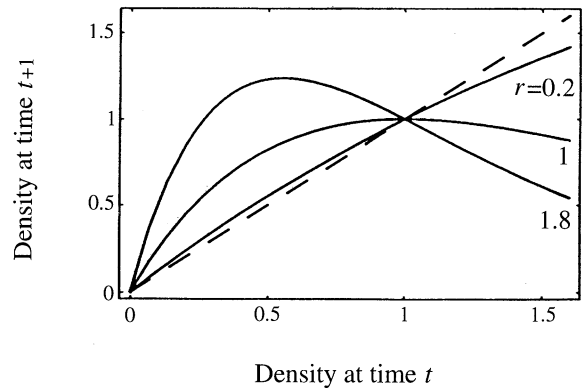


FIG. 1. The population density at time $t+1$ vs. the density at time t for Eq. 2 with stochasticity removed. r determines the strength of density dependence. Values of μ equal r to give deterministic equilibrium population densities of one.

of $r = 0.2$, 1, and 1.8 will be used throughout this example. The dynamics produced by Eq. 2 are given in Fig. 2. Fig. 2d shows $u(t)$ vs. t for 100 time units. For the first 50 time units, the mean of $u(t)$ is zero, and at $t = 51$ the mean increases to 0.2. Fig. 2a-c shows the population densities given by Eq. 2 with $r = 0.2$, 1, and 1.8, respectively, subject to the same pattern of environmental stochasticity, $u(t)$ and $\omega(t)$. As the mean of $u(t)$ increases, so do mean population densities, and the magnitude of the change depends on the strength of density dependence, r ; the weaker the density dependence (smaller values of r), the greater the change in mean density. As shown in Fig. 2c, increasing the mean of $u(t)$ may also affect the variance in population densities. Here, the increase in $u(t)$ produces strong overcompensating population dynamics; in the deterministic counterpart of the model, removing the variance in $u(t)$ and $\omega(t)$, the population dynamics become unstable when the mean of $u(t)$ increases by 0.2.

Fig. 3 shows the same data as Fig. 2, but in a manner to highlight the difference between short-term and long-term population responses to environmental variability. Each graph in Fig. 3 shows the relationship between $n(t+1)$ and $u(t)$ for $t = 1-100$. When there is weak density dependence (Fig. 3a), the change in the population density from the first to the second sets of 50 time units is greater than the change within each set in response to $u(t)$. The opposite is true when density dependence is strong (Fig. 3c). Therefore, stronger density dependence produces negative feedback against long-term changes in population densities. This gives a warning: the population responses to short-term environmental fluctuations may give poor estimates of the responses to long-term environmental trends, since the long-term changes depend on feedbacks operating through density-dependent population dynamics.

Predicting changes in mean population density

There are several ways in which data in the form of Eq. 1 could be analyzed to predict changes in mean

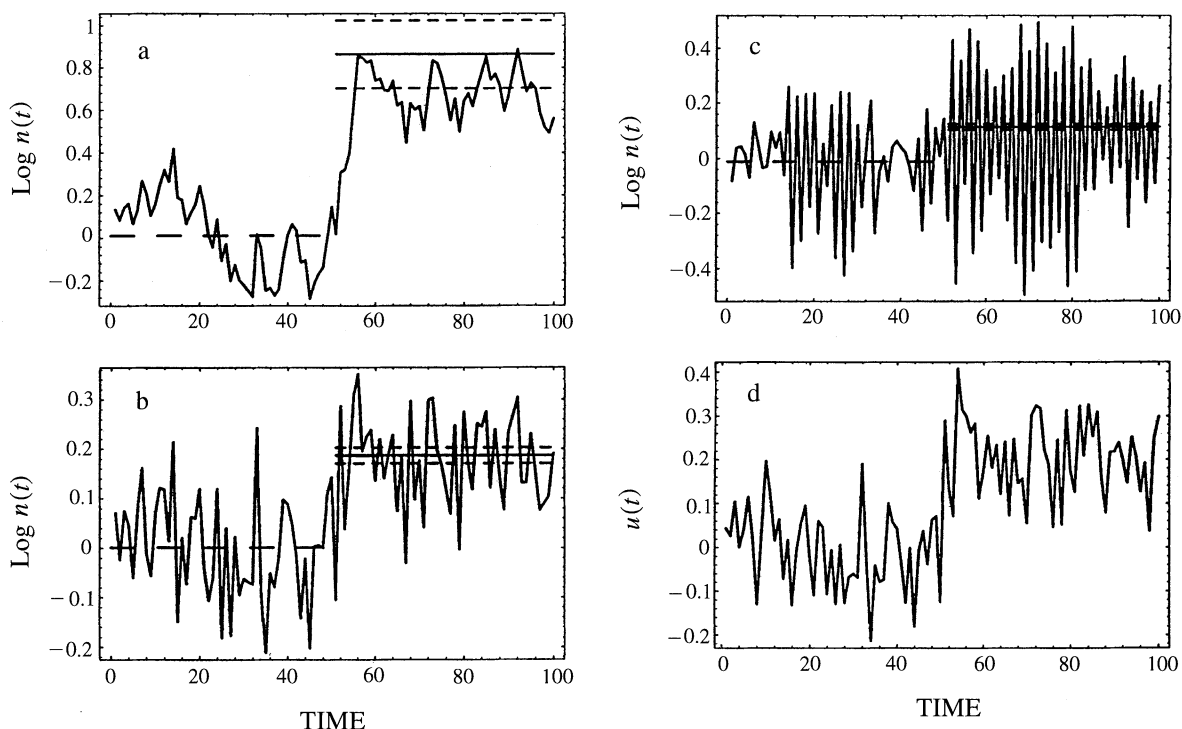


FIG. 2. (a)–(c) Changes in the population density $n(t)$ through time for (a) $r = 0.2$, (b) 1.0, and (c) 1.8. (d) The environmental variable $u(t)$ vs. time. At $t = 50$ the mean value of $u(t)$ increases from 0 to 0.2. In (a)–(c), the dashed line for $t = 1, \dots, 50$ gives the mean population density. The solid line for $t = 51, \dots, 100$ is the predicted mean density (Eq. 5) following the increase in the mean of $u(t)$; dashed lines give the standard errors of the predictions obtained from jackknifing. In all graphs $\omega(t)$ has mean 0 and variance 0.1.

population densities with long-term trends in $u(t)$. The most direct is to find the best-fitting nonlinear model for the data and to use this in estimating the consequences of environmental changes. However, distinguishing the best-fitting nonlinear model may be difficult, and the best-fitting model may not necessarily give the best predictions of changes in mean population density; this is discussed in the next section. Furthermore, the problem of fitting nonlinear models is greatly compounded when analyzing multispecies data sets. The approach I have adopted here is to fit linear models to data, even though the data are most likely nonlinear. An advantage of this approach is that it reveals in a heuristic fashion how density dependence affects the response of population densities to environmental trends.

To begin, data in the form of Eq. 1 can be fit to the linear regression equation

$$n(t+1) = au(t) + b_0 + (b_1 + 1)n(t) + \epsilon[t, n(t)]. \quad (3)$$

In applying linear regression, $n(t)$ and $u(t)$ can be transformed to increase linearity. Regression coefficients a , b_0 , and b_1 are calculated from least squares in the standard fashion. As an important departure from standard regression, the “error term” $\epsilon[t, n(t)]$ is assumed to depend on $n(t)$. The term $\epsilon[t, n(t)]$ incorporates not only variability in the population growth rate driven by en-

vironmental variability other than that captured by $u(t)$, but also variability in the population growth rate caused by the residual nonlinear effects $n(t)$ after the linear effects are extracted. Thus, Eq. 3 can be regarded as a reformulation of Eq. 1, rather than a linear approximation.

Eq. 3 is a phenomenological description of the population dynamics observed in a data set. The regression coefficient a corresponds to the magnitude of the effect of $u(t)$ on the population growth rate, and b_1 gives the strength of density dependence in terms of the effect of density on the per capita population growth rate. These regression coefficients are population-level descriptors, and as such they cannot be interpreted in terms of particular life history characteristics. However, the objective here is to make population-level predictions about the response of population density to environmental trends, and therefore population-level descriptors of population dynamics are appropriate. The aim of previous theoretical studies has been to relate life history characteristics to stochastic population dynamics; for example, May (1973), Turelli (1977), Pimm (1982), and others have asked how variability in r vs. K affects the variance in population densities in stochastic Lotka-Volterra equations. Since these studies are explicitly designed to analyze life history characteristics, their parameters must be defined

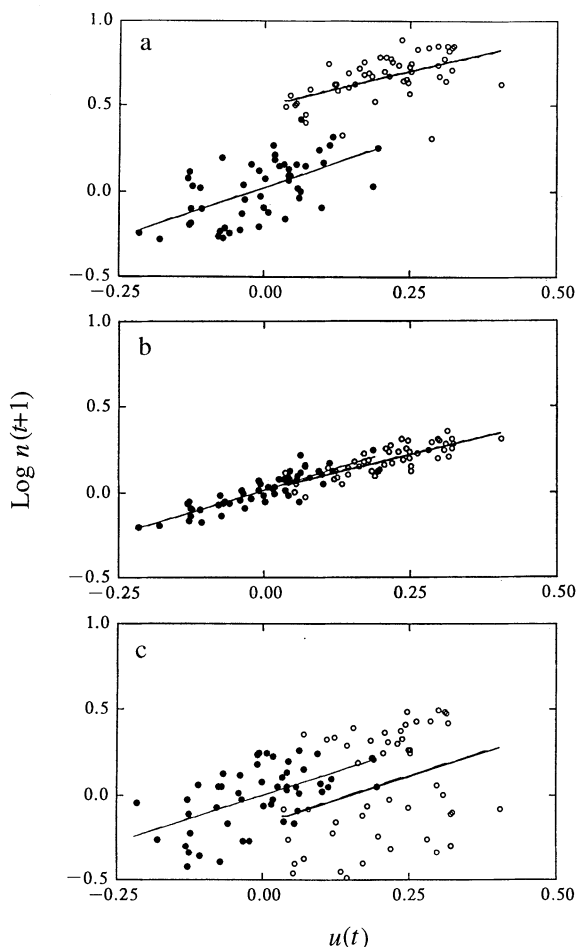


FIG. 3. Population densities $n(t+1)$ vs. $u(t)$ for (a) $r = 0.2$, (b) 1.0 , and (c) 1.8 . These are the same data as in Fig. 2. Solid circles correspond to data from $t = 1, \dots, 50$, and open circles are for data from $t = 51, \dots, 100$. Regression lines were fit to data before and after the change in the mean of $u(t)$.

as life history characteristics. For making population-level predictions about responses to environmental trends, an advantage of using the regression coefficients a and b_1 is that they summarize the sensitivity of population growth rates to environmental variability (a) and density dependence (b_1) in a general manner. There is no need to impose a particular equation, such as the Lotka-Volterra equation, on the data set.

The problem of how mean population densities respond to environmental trends requires calculating the change in the stationary population distribution resulting from changes in the distribution of $u(t)$. The stationary population distribution is the distribution that would be produced if population densities were accumulated for an infinitely long time (Turelli 1977, 1978). For any finite data set, the mean population density might not exactly equal the mean of the theoretical stationary population distribution, since the va-

garies of stochastic processes may produce relatively high or low population densities in a finite data set. However, the mean of the stationary population distribution gives the expected mean population density.

Let N denote the mean density of the stationary population distribution when the random variable $u(t)$ has a mean of U . The problem is to calculate how N changes with changes in U . At the stationary population distribution, $E[n(t+1)] = E[n(t)] = N$, since there are an infinite number of samples. Therefore, taking the mean of both sides of Eq. 3 and solving for N gives $N = -(aU + b_0)/b_1$. If the mean value of U changes to U' , the corresponding mean population density is $N' = -(a'U' + b_0')/b_1'$. Due to the nonlinearity in the relationship between the population growth rate and $n(t)$, the regression coefficients a , b_0 , and b_1 at the new mean U' may be different from those generated for U and are therefore marked by apostrophes. Writing $\Delta N = N' - N$ and $\Delta U = U' - U$,

$$\Delta N = \frac{a\Delta U + \Delta a\Delta U + \Delta aU + \Delta b_0 - \Delta b_1N}{b_1 + \Delta b_1}. \quad (4)$$

Thus, the change in mean population density depends on changes in the mean of the environmental parameter ΔU and changes in the regression coefficients, $\Delta a = a' - a$, $\Delta b_0 = b_0' - b_0$, and $\Delta b_1 = b_1' - b_1$. If Δa , Δb_0 , and Δb_1 are small, Eq. 4 reduces to

$$\Delta N \approx -\Delta U a/b_1. \quad (5)$$

This approximation is essentially an extrapolation from the observed pattern of population dynamics to a new pattern when the mean of the environmental variable $u(t)$ changes. The extrapolation will be good provided the regression coefficients a' , b_0' and b_1' under the new environmental regime are similar to those in the old environmental regime. However, strong nonlinearities in the relationship between the population growth rate and $n(t)$ may result in significant changes in the regression coefficients if there are large changes in U . The accuracy of the approximation depends not just on the degree of nonlinearities in the population growth rate, but also on the naturally occurring short-term variability in population density. If the short-term variability is large relative to the long-term change in the environmental mean, then nonlinearities in the population growth rate are "averaged out" when applying linear regression. With large short-term variability, approximation 5 has more the character of interpolation than of extrapolation.

Approximation 5 has the following biological interpretation. If the environmental stressor $u(t)$ has a large effect on the population growth rate (a is large) then the mean population density is more sensitive to changes in U . However, strong density dependence given by the coefficient b_1 buffers the mean population density against changes in U . This is because density dependence acts as a negative feedback against changes in densities. Although this conclusion is neither new

nor surprising, linear regression and approximation 5 give a simple way to quantify the relative effects of environmental change and density dependence on changes in mean population densities.

Applying the prediction to the simulated data set

There are two components to the accuracy of the predictions made by Eq. 5: how nonlinearities in the population dynamics affect the expectation of the change in mean population densities, and how the precision of the estimated regression coefficients affects the precision of the predicted changes in mean population densities. These two components are examined below for the simulated single-species data sets.

The stationary population distribution of Eq. 2 can be calculated numerically as an integral equation (Ives and Gilchrist 1993). This makes it possible to calculate directly the relationship between changes in the mean of $u(t)$ and changes in mean population density at the stationary distribution. Fig. 4a–c gives the observed and predicted changes in the mean of the stationary population distribution with changes in the mean of $u(t)$ for $r = 0.2, 1$, and 1.8 , respectively. The regression coefficients used in Eq. 5 are calculated from the stationary population distribution. Because the stationary population distribution has an infinite number of sample points, the estimates of regression coefficients are perfectly precise. Therefore, the difference between the observed and predicted changes in mean population density result only from nonlinearities in the population dynamics, not from imprecision in the estimates of the regression coefficients. As shown from Fig. 4, nonlinearities in the population dynamics tend to make Eq. 5 underestimate the changes in mean population densities. Nonetheless, the predictions are still quite good.

The problem of fitting a model to a finite data set can be illustrated by applying Eq. 5 directly to the simulated data. Imprecision in the predictions due to imprecision in the estimated regression coefficients a and b_1 can be ascertained through jackknifing. Jackknifing involves calculating a statistic (in this case, a/b_1) for a given data set multiple times, each time removing a different subset of points from the data (Sokal and Rohlf 1981). To jackknife the simulated data sets, I calculated a/b_1 50 times, removing successively each set of points $[n(t+1), n(t), u(t)]$ for $t = 1, \dots, 50$ from the linear regression model. From these it is possible to calculate the expectation and standard error of the statistic a/b_1 , where the standard error is distributed according to a t distribution with 49 degrees of freedom. Fig. 2a–c shows the predicted mean population densities (solid line) with their standard errors (dashed lines) for time $t = 51, \dots, 100$.

The estimated mean population densities in Fig. 2 include both inaccuracies due to the application of linear regression to nonlinear population dynamics and imprecision due to the estimates of regression coefficients.

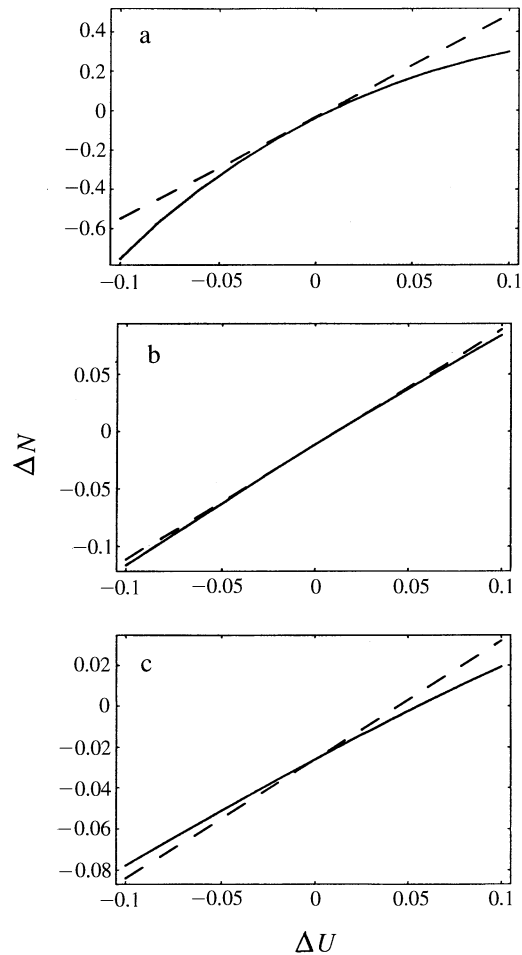


FIG. 4. Change in the mean log population density with changes in the mean value of $u(t)$ for (a) $r = 0.2$, (b) 1.0 , and (c) 1.8 . Solid lines give the true change in the mean of the stationary population distribution calculated analytically, and the dashed lines give the predictions from Eq. 5 made when the mean value of $u(t)$ is zero.

cients. In all three cases, the estimated mean population density is greater than the observed due to nonlinear population dynamics (Fig. 4). Imprecision of the predicted mean population densities due to imprecise estimates of the regression coefficients is greater when density dependence is weak (Fig. 2a), since weak density dependence makes it more difficult to quantify the strength of intraspecific interactions. Overall, the accuracy of the predictions from Eq. 5 is not perfect, but it is quite reasonable given the uncertainties that ecologists must routinely face.

One could argue that applying a nonlinear model to the data will improve the prediction. However, this depends on how well a nonlinear model can be fit to the data. Table 1 shows the predictions made by fitting four different nonlinear models to the simulated data. The models are standard single-species equations used by a variety of authors (May 1981); model M1 has the

TABLE 1. Predicted changes in mean log density for data simulated by Eq. 3.

	$r = 0.2$		$r = 1$		$r = 1.8$	
	ΔN	R^2	ΔN	R^2	ΔN	R^2
Observed*	0.662		0.176		0.0748	
Linear†: $n(t)e^{b_0+au(t)}n(t)^{b_1}$	0.852	0.931	0.186	0.794	0.125	0.904
	± 0.160		± 0.016		± 0.011	
M1: $n(t)e^{b_0+au(t)+b_1n(t)}$	0.637	0.931	0.170	0.807	0.103	0.938
M2: $n(t)e^{b_0+au(t)}/[1+b_1n(t)]$	0.683	0.931	0.205	0.780	0.217	0.295
M3: $n(t)e^{b_0+au(t)}[1+b_1n(t)]$	0.592	0.931	0.156	0.809	0.077	0.859
M4: $n(t)e^{b_0+au(t)}[1+b_1n(t)+b_2n(t)^2]$	1.59	0.931	0.095	0.810	0.0989	0.939

* The observed change in mean log density is calculated as the mean of the first 50 data points subtracted from the mean of points 61–100; the first 10 points after the change in $u(t)$ are excluded to remove transients.

† This is a linear regression model when population densities are log-transformed.

same form as Eq. 2 used to generate the simulated data set. Models M1–M4 were fit to the first 50 data points in the simulated data shown in Fig. 2 after log-transforming population density. The predicted change in mean population density was then calculated from the fitted equations. When density dependence is weak ($r = 0.2$), all four nonlinear models and the linear model (Eq. 3) fit the data equally well, although there is a range of the predicted changes in mean population density. For stronger density dependence, the models that fit the data best do not necessarily produce the best predictions for changes in mean population densities. The message from this exercise is that selecting a best-fitting nonlinear model will not necessarily produce more accurate predictions of changes in mean population densities. Since there is a large number of possible nonlinear models to choose from, trying to account for nonlinearities may confuse rather than clarify

the predictions. The simpler approach advocated here is to use linear regression and realize that this will generally lead to overestimates in the predicted changes in mean population densities.

MULTISPECIES DATA

For a species embedded in an ecological community, the response of the population to environmental change will depend in a complex way on the web of interactions among species. The data analyzed in this section for a community of S species have the general form

$$n_i(t+1) = f_i[n_1(t), n_2(t), \dots, n_S(t), u(t), \omega_i(t)] \quad (6)$$

where $n_i(t)$ is the population density of species i in sample t , and f_i is its population growth rate. f_i depends on the densities of all S species in the community, the environmental variable $u(t)$ which undergoes a directional change in mean or variance, and the random variable $\omega_i(t)$ summarizing all of the environmental variability not included in $u(t)$. Since the environmental changes may affect different species differently, the dependence of f_i on $u(t)$ may be different for each species. Also, species may be affected by different environmental factors, so $\omega_i(t)$ may be different for each species.

The problem in this section is the same as in the single-species case: how do changes in the mean of $u(t)$ change the mean abundance of each species in the community?

Simulated four-species example

In this section I construct a four-species simulated data set that I will then use to illustrate the prediction techniques developed in subsequent sections. The four-species simulated data set is not meant to be realistic by incorporating many details that might be found in a real biological system. However, it is moderately complex and therefore presents a considerable challenge to the prediction techniques.

The four-species model consists of three competitors and a predator that attacks two of the competitors. Fig. 5 shows a food web of the system. The competitors have discrete-time Lotka–Volterra dynamics, and the

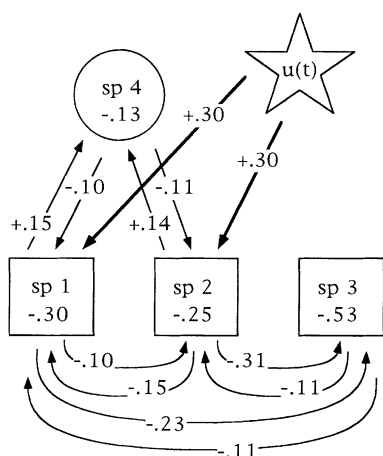


FIG. 5. Diagram of the community described by the simulation model (Eq. 7). Interaction strengths among species shown in the graph are calculated as the change in population growth rate of species i with changes in population density of species j calculated at equilibrium for the deterministic version of Eq. 7. Numbers within the species squares (competitors) or circle (predator) give the strength of intraspecific interactions. The heavy arrows give the effect of the environmental factor $u(t)$.

predator has a Type II functional response (Holling 1959) and additional intraspecific density dependence that might occur if it had prey other than the two species of competitors explicitly modeled in the system. The equations governing the population dynamics are

$$\begin{aligned}
 n_1(t+1) &= n_1(t)e^{\mu_1+q_1u(t)+\omega_1(t)} \\
 &\quad \times \left\{ \left[1 - \alpha_{11}n_1(t) - \alpha_{12}n_2(t) - \alpha_{13}n_3(t) \right] \right. \\
 &\quad \left. - \frac{c_{14}n_4(t)}{1 + c_{14}h_{14}n_1(t)} \right\} \\
 n_2(t+1) &= n_2(t)e^{\mu_2+q_2u(t)+\omega_2(t)} \\
 &\quad \times \left\{ \left[1 - \alpha_{21}n_1(t) - \alpha_{22}n_2(t) - \alpha_{23}n_3(t) \right] \right. \\
 &\quad \left. - \frac{c_{24}n_4(t)}{1 + c_{24}h_{24}n_2(t)} \right\} \\
 n_3(t+1) &= n_3(t)e^{\mu_3+\omega_3(t)} \{ [1 - \alpha_{31}n_1(t) - \alpha_{32}n_2(t) \\
 &\quad - \alpha_{33}n_3(t)] \} \\
 n_4(t+1) &= n_4(t)e^{\mu_4+\omega_4(t)} \\
 &\quad \times \left\{ \left[1 - \alpha_{44}n_4(t) \right] + \frac{g_1c_{14}n_1(t)}{1 + c_{14}h_{14}n_1(t)} \right. \\
 &\quad \left. + \frac{g_2c_{24}n_2(t)}{1 + c_{24}h_{24}n_2(t)} - d_4 \right\}. \quad (7)
 \end{aligned}$$

Here, $n_1(t)$, $n_2(t)$, and $n_3(t)$ are the densities of the competitors at time t , and $n_4(t)$ is the density of the predator. For species 1 and 2, the density-independent per capita population growth rate, $e^{\mu_i+q_iu(t)+\omega_i(t)}$ ($i = 1, 2$), depends on the constant μ_i , the environmental variable $u(t)$ scaled by q_i , and a random variable $\omega_i(t)$ to account for environmental variability other than that produced by $u(t)$. For species 3 and 4, the density-independent per capita population growth rates are similar but do not depend on $u(t)$. For all four species, the random variables $\omega_i(t)$ are assumed to follow independent normal distributions, and because they appear as exponential terms, the per capita population growth rate is lognormally distributed. For the competitors, intra- and interspecific competition are governed by the terms $-\alpha_{ij}n_j(t)$, which give the decrease in the population growth rate of species i with changes in the density of species j . The per capita predation rate on species 1 and 2 is given by the Type II functional response $c_{i4}n_4(t)/[1 + c_{i4}h_{i4}n_i(t)]$ ($i = 1, 2$), where c_{i4} scales the overall attack rate, and h_{i4} determines the strength of nonlinearity in the functional response. The larger the value of h_{i4} , the more rapidly the per capita predation rate decelerates with increasing prey density. In the predator population growth rate, g_i ($i = 1, 2$) scales the conversion of depredated prey into predator reproduction. The predator experiences intraspecific competi-

tion through the term $\alpha_{44}n_4(t)$, and there is a density-independent per-capita death rate of d_4 .

To add complexity to the environmental variable $u(t)$, I assume that it is temporally autocorrelated. Specifically, $u(t) = m \cos(2\pi t/p) + \eta(t)$ where p is the period and m is the amplitude of the autocorrelated component of $u(t)$, while $\eta(t)$ is a random variable adding uncorrelated variability to $u(t)$. For the simulation example, $p = 10$, which corresponds to the case in which $u(t)$ shows seasonal fluctuations and population densities are sampled 10 times each year. Eq. 7 might be a model for terrestrial insects such as aphids and parasitic wasps that have multiple overlapping generations per year, or species of herbivorous and carnivorous zooplankton.

Fig. 6a-d shows the population densities of the four species for 20 yr (200 iterations of Eq. 7), and Fig. 6e shows values of $u(t)$. For the first 10 yr the annual mean of $u(t)$ equals 0, and at $t = 100$ it increases to 1.5. In response, population densities of all four species increase or decrease. Fig. 7 shows the same data as Fig. 6, but population densities $n_i(t+1)$ are graphed against $u(t)$. Black dots correspond to the first 10 yr and gray dots correspond to the second 10 yr, with regression lines fitted to each set of points. For both species 1 and 2, q_i is positive, so increases in $u(t)$ increase their per-capita population growth rates. This is seen in the positive slopes of the regressions of $n_i(t+1)$ vs. $u(t)$. However, with the increase in the mean of $u(t)$ at $t = 100$, the mean density of species 1 decreases. This shows that the response of populations to short-term environmental fluctuations may be very different from the response to long-term environmental trends, due to the feedbacks operating through the interactions among species. An explanation for the response of species 1 is given in detail in *The pattern of environmental and species interactions*.

Predicting changes in mean population density

The approach to the multispecies case is the same as for the single-species case. Rather than try to construct a complicated mechanistic model and estimate its numerous parameters, instead I apply simple linear regression to data in the form of Eq. 6. The linear reformulation of Eq. 6 is

$$\begin{aligned}
 n_i(t+1) &= a_i u(t) + b_{i0} + \epsilon_i(t, n_1, n_2, \dots, n_s) \\
 &\quad + n_i(t) + \sum_{j=1}^s b_{ij} n_j(t). \quad (8)
 \end{aligned}$$

As in Eq. 3, the terms a_i and b_{ij} are least squares regression coefficients, and ϵ_i is an "error term" that includes both environmental variability not associated with the environmental parameter $u(t)$ and variability due to the nonlinear component of interactions among species. The problem is to estimate the change in the mean of the stationary population distribution of species i when the mean of $u(t)$ changes.

Taking the expectation of both sides of Eq. 8 for all

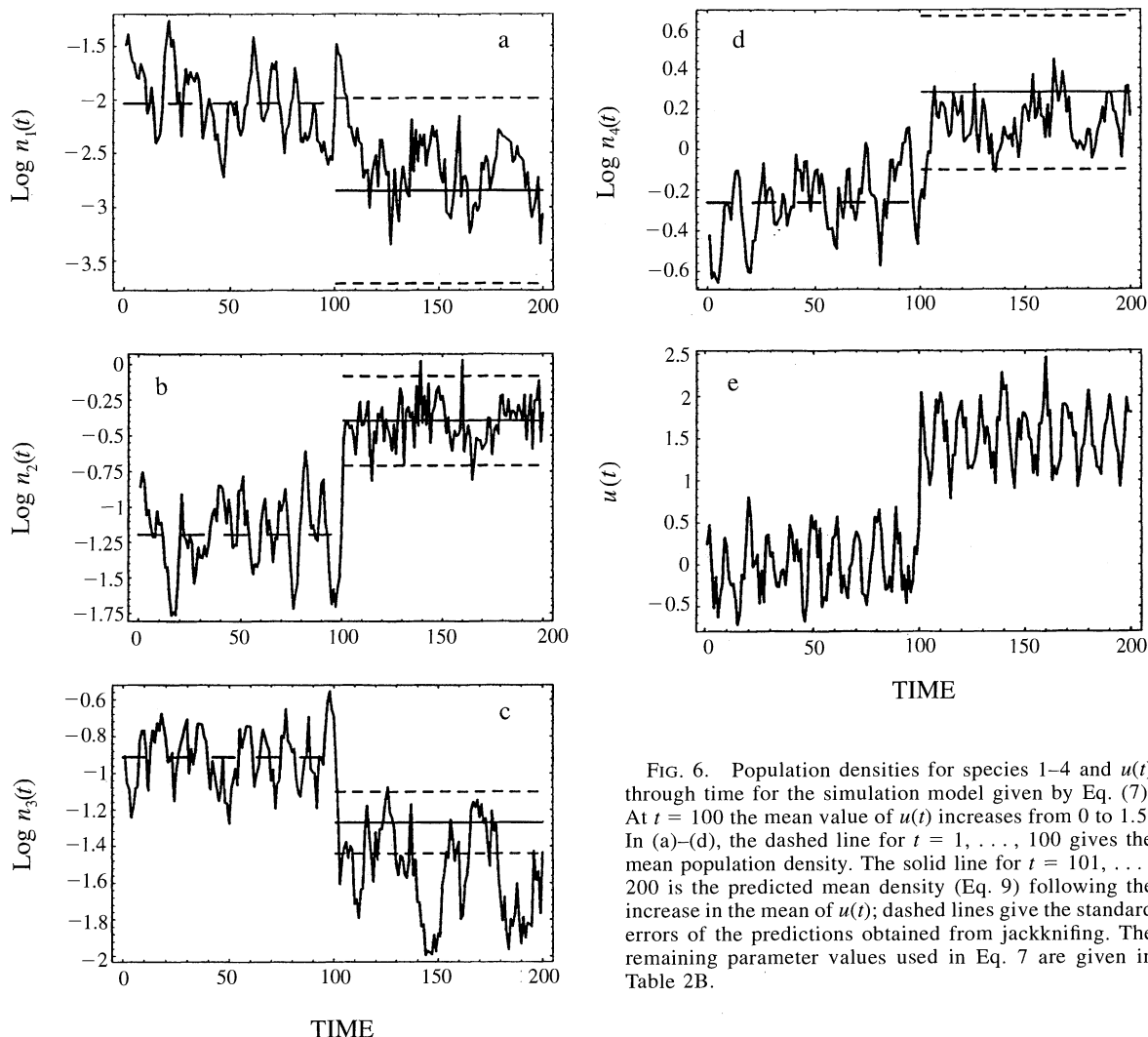


FIG. 6. Population densities for species 1-4 and $u(t)$ through time for the simulation model given by Eq. (7). At $t = 100$ the mean value of $u(t)$ increases from 0 to 1.5. In (a)-(d), the dashed line for $t = 1, \dots, 100$ gives the mean population density. The solid line for $t = 101, \dots, 200$ is the predicted mean density (Eq. 9) following the increase in the mean of $u(t)$; dashed lines give the standard errors of the predictions obtained from jackknifing. The remaining parameter values used in Eq. 7 are given in Table 2B.

S species in the community gives a set of S equations with S unknown values of the mean population densities for each species. Solving these equations for two different values of the mean environmental parameter, U and U' , and assuming that the difference between the regression parameters a_i and b_{ij} for U and U' are negligible, gives the following solution for the change in mean population density of species i , ΔN_i , for a given change in the mean value of $u(t)$, ΔU (Apostol 1969):

$$\Delta N_i = -\Delta U \frac{\det(\mathbf{B}_1, \dots, \mathbf{B}_{i-1}, \mathbf{A}, \mathbf{B}_{i+1}, \dots, \mathbf{B}_S)}{\det(\mathbf{B}_1, \mathbf{B}_2, \dots, \mathbf{B}_S)}, \quad (9)$$

where

$$\mathbf{A} = [a_1, a_2, \dots, a_S],$$

$$\mathbf{B}_j = [b_{1j}, b_{2j}, \dots, b_{Sj}],$$

and $\det()$ represents the determinant of the matrix composed of the specified vectors. In biological terms, the vector \mathbf{B}_j measures the effect of species j on all of the

other species in the community. Since \mathbf{B}_j measures the sign and magnitude of interactions that species j has with other species, we can describe the ecological role of species j as the pattern given by \mathbf{B}_j . The vector \mathbf{A} measures the effect of the environmental parameter $u(t)$ on all of the species in the community. Thus, the denominator of Eq. 9 is the determinant of the matrix describing all ecological interactions in the community, while the numerator is the determinant of the matrix in the denominator, but with the effects of species j on all other species replaced with the effect of the environmental stressor on the population growth rates of these species. Eq. 9 is simply a statement of "Cramer's Rule" (Apostol 1969) which has been used in deterministic community models in a number of contexts (Levins 1975, Levine 1976, Harrison and Fekete 1980, Oksanen et al. 1981, Yodzis 1989, Puccia and Levins 1991).

Fig. 6 shows the predicted change in mean population density for each species given by Eq. 9 as a solid

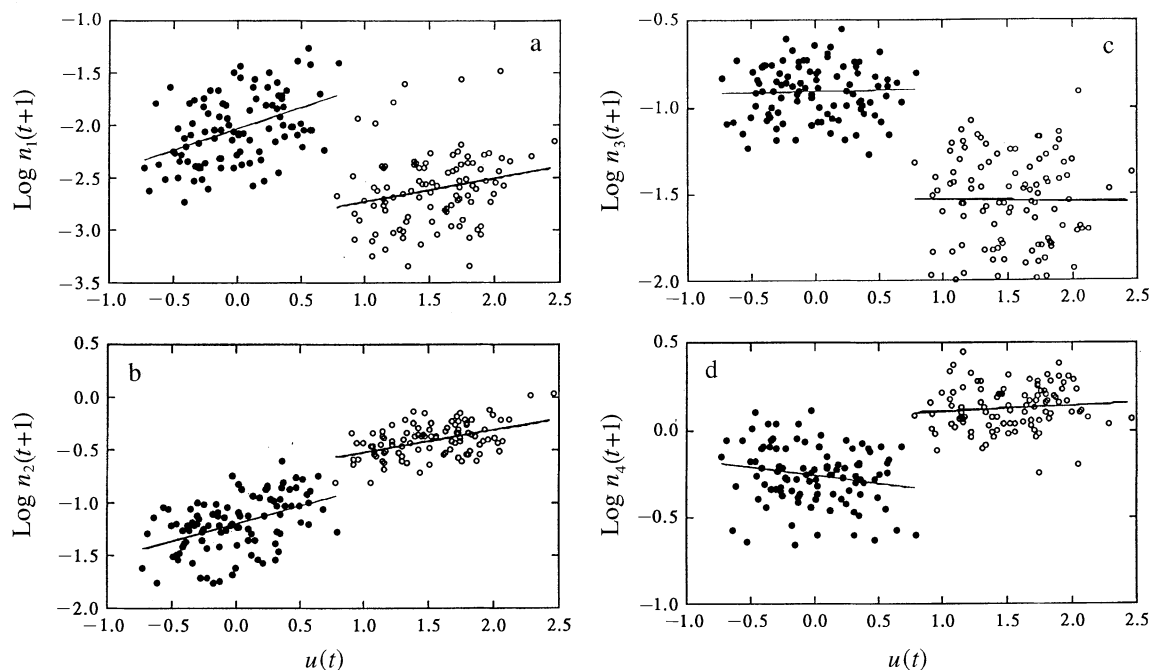


FIG. 7. Population densities $n(t+1)$ vs. $u(t)$ for (a) species 1, (b) species 2, (c) species 3, and (d) species 4. These are the same data as in Fig. 6. Solid circles correspond to data from $t = 1, \dots, 100$, and open circles are for data from $t = 101, \dots, 200$. Regression lines were fit to data before and after the change in the mean of $u(t)$.

line. In applying the regression model of Eq. 8, coefficients for nonexistent interactions in the food web (Fig. 5) were set to zero ($b_{34} = b_{43} = a_3 = a_4 = 0$). Jackknifing was used to calculate standard errors of the estimate in the same manner as for the single species. As shown by the graphs, the predicted changes in mean densities are reasonably good, although the method underestimates the changes in mean densities for species 1 and 3. The standard errors indicate that some of the underestimation might come from imprecision in the estimates of the regression coefficients, although nonlinearities in the model given by Eq. 7 also play a part. Because the stationary population distribution for Eq. 7 cannot be solved numerically, it is impossible to determine exactly how nonlinearities affect changes in mean population densities. Finally, species 1 is on the verge of extinction; an increase in the mean of $u(t)$ by an additional 0.5 leads species 1 to go extinct. Because the data used in the regression model were first log transformed, Eq. 9 will not predict the extinction of species, since this corresponds to densities of minus infinity. However, applying Eq. 9 to untransformed data does predict the extinction of species 1 for larger increases in the mean of $u(t)$. Thus, to predict extinctions it is best to use untransformed data.

One might suspect that fitting an appropriate nonlinear model to the data set will improve the predictions for changes in mean population densities. In fact, this is not necessarily the case. I fit the first 10 yr of data to a nonlinear least squares regression model (Wilkin-

son 1987) having the same structure as Eq. 7, the equation used to generate the simulated data. Nonlinear regression gave nonsensical negative values for the parameters h_{14} and h_{24} , so I set these parameters to zero. This removes the Type II functional response from the nonlinear regression model. After fitting the other parameters, I solved Eq. 7 numerically to give the population densities before and after the change in the mean of $u(t)$ assuming no environmental variability. When the mean of $u(t)$ equals 1.5, the fitted equations predict that species 1 goes extinct. However, simulating the case in which $u(t)$ varies cyclically ($m = 0.4$, $p = 10$) but not stochastically (variances in $\omega_i(t)$ and $\eta(t)$ equal zero) produced persistence of species 1, so changes in mean density were determined from the numerical simulations. Table 2A gives the predicted changes in mean population densities calculated from nonlinear and linear regression (Eq. 9). For species 2, 3, and 4, the predictions from both techniques are similar, although Eq. 9 does slightly better. For species 1, Eq. 9 is considerably more accurate.

This result might seem peculiar, since the nonlinear regression model should capture the dynamics of the simulated data better than linear regression. However, parameters in a nonlinear regression model may be difficult to estimate. Table 2B gives the estimated parameters from nonlinear regression to compare with the parameters used in the simulation. Some of the estimated parameters are far from their true values, especially α_{21} , α_{31} , g_1 , and d_4 . The advantage of linear

TABLE 2. (A) Observed and predicted changes in mean log population density using two prediction methods for the four-species simulation data.

Species	Observed ΔN	Predicted from linear regression (Eq. 9)	Predicted from nonlinear regression
1	-0.57	-0.82 ± 0.86	-0.026
2	0.79	0.80 ± 0.31	0.50
3	-0.62	-0.36 ± 0.17	-0.33
4	0.39	0.54 ± 0.38	0.28

(B) True values of parameters in Eq. 7 and estimates from nonlinear regression.

Para.	Value	Est.	Para.	Value	Est.	Para.	Value	Est.	Para.	Value	Est.
μ_1	0.9	0.88	μ_2	0.6	0.73	μ_3	0.6	0.63	μ_4	0.1	0.12
q_1	0.3	0.17	q_2	0.3	0.28	α_{31}	0.3	0.12	α_{44}	0.15	0.25
α_{11}	0.8	0.93	α_{21}	0.2	0.52	α_{32}	0.4	0.46	g_1	0.6	-0.63
α_{12}	0.4	0.43	α_{22}	0.5	0.60	α_{33}	0.7	0.76	g_2	0.8	0.95
α_{13}	0.3	0.15	α_{23}	0.3	0.112				d_4	0.05	0.0013
c_{14}	0.3	0.33	c_{24}	0.2	0.27						
h_{14}	0.1	0*	h_{24}	0.1	0*						

* Estimated values set to zero; otherwise, nonsensical values are produced.

regression is that the regression parameters enter as additive terms, which tends to make estimates much more robust.

The pattern of environmental and species interactions

Although Eq. 9 gives a mathematical prediction about changes in mean population densities, its biological interpretation is opaque. However, it can be expressed in a manner that brings out biologically meaningful patterns. This is done by noting the geometrical interpretation of determinants. Several definitions are necessary. First, $\|\mathbf{B}_j\|$ denotes the magnitude of \mathbf{B}_j defined by $(b_{1j}^2 + b_{2j}^2 + \dots + b_{sj}^2)^{1/2}$. The angle

β_j is the angle between vector \mathbf{B}_j and the vector orthogonal to the surface defined by all the vectors \mathbf{B}_i excluding \mathbf{B}_j . For the case of a three-species community, Fig. 8 illustrates the angle β_1 . This angle gives a composite measure of how similar the ecological role of species j is compared to the ecological roles of other species in the community. Values of β_j close to zero or 180° (\mathbf{B}_1 almost orthogonal to the plane in Fig. 8) correspond to the case when species j has distinctly different patterns of interactions with other species. Values of β_j close to 90° (\mathbf{B}_1 almost in the plane in Fig. 8) imply that species j has the same ecological impact on other species as some other species or combination of species in the community. Finally, the angle α_j is the angle between vector \mathbf{A} and the vector orthogonal to the surface defined by all the vectors \mathbf{B}_i excluding \mathbf{B}_j (Fig. 8). As with β_j , α_j measures how similar the effects of changing the mean value of $u(t)$ is to changing the densities of any species other than species j .

With these definitions, Eq. 9 can be written

$$\Delta N_j = -\Delta U \frac{\|\mathbf{A}\| \cos \alpha_j}{\|\mathbf{B}_j\| \cos \beta_j}. \quad (10)$$

This equation can be most easily understood by noting that the numerator and denominator are the projections of the vectors \mathbf{A} and \mathbf{B}_j , respectively, onto the vector orthogonal to the plane defined by \mathbf{B}_i ($i \neq j$). Eq. 10 collapses the multispecies system into a single dimension by rotating the axes of orientation. In the single-species system analyzed previously, the change in mean population density depends on the regression coefficients a and b_1 (Eq. 5). In Eq. 10, $\|\mathbf{A}\| \cos \alpha_j$ and $\|\mathbf{B}_j\| \cos \beta_j$ serve the same roles as a and b_1 , respectively.

Eq. 10 can be understood by noting that following an environmental change, mean population densities of all species in a community must change to return the mean population growth rates of all species to one. For species that exert a strong effect on population growth rates ($\|\mathbf{B}_j\|$ large), relatively small changes in mean den-

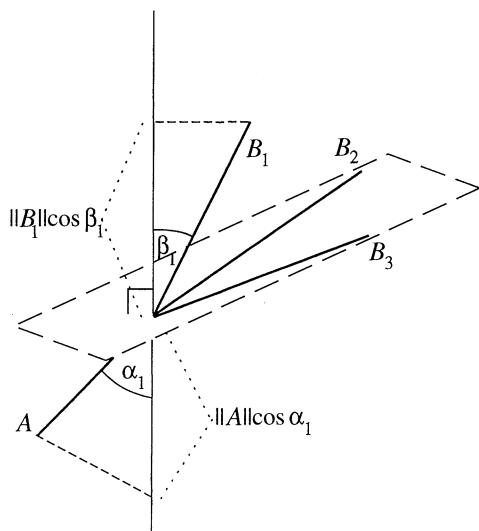


FIG. 8. Diagram giving a graphical interpretation of Eq. 10 for a three-species community. Vectors \mathbf{B}_i are defined by the points $[b_{1i}, b_{2i}, b_{3i}]$, and \mathbf{A} is defined by $[a_1, a_2, a_3]$. The quantities $\|\mathbf{B}_1\| \cos \beta_1$ and $\|\mathbf{A}\| \cos \alpha_1$ are the projections of \mathbf{B}_1 and \mathbf{A} onto the vector orthogonal to the surface spanned by \mathbf{B}_2 and \mathbf{B}_3 .

TABLE 3. (A) Patterns of interactions for the simulated data from Eq. 7.

Species	$-\frac{\ \mathbf{A}\ \cos\alpha}{\ \mathbf{B}_j\ \cos\beta}$	$\cos\alpha_j$	$\ \mathbf{B}_j\ $	$\cos\beta_j$
1	-0.82	0.24	0.35	0.29
2	0.80	-0.52	0.53	0.51
3	-0.36	0.35	0.61	0.68
4	0.54	-0.32	0.73	0.30

(B) Regression coefficients for the first 100 points of simulated data from Eq. 7.

Species	b_{i1}	b_{i2}	b_{i3}	b_{i4}	a_i
1	-0.32	-0.27	-0.097	-0.59	0.15
2	-0.12	-0.33	-0.052	-0.36	0.25
3	-0.012	-0.28	-0.60	0	0
4	-0.033	0.13	0	-0.23	0

sity have large effects on population growth rates. This reduces the change in the mean density of species j needed to counteract the environmental change. Species that occupy distinct ecological roles in the community ($\cos\beta_j$ large) are also buffered against changes in mean density because they cannot easily supplant or be supplanted by other species in the community. Finally, the change in the mean population density of species j will be small when the pattern of effects of $u(t)$ on population growth rates is similar to the patterns exerted by other species in the community ($\cos\alpha_j$ small). This is because changes in population growth rates brought about by the environmental change can be offset by changes in mean densities of species in the community other than species j .

Table 3A gives values of $\|\mathbf{B}_j\|$, $\cos\alpha_j$, and $\cos\beta_j$ for each of the four species whose dynamics are given by Eq. 7. Table 3B gives the regression coefficients calculated from the model of Eq. 8; b_{ij} gives the effect of species j on the population growth rate of species i , and the vectors \mathbf{B}_i are the columns in the table. Mean population densities decrease following an environmental change if the projections of \mathbf{A} and \mathbf{B}_j onto the vector orthogonal to \mathbf{B}_i ($i \neq j$) have the same sign (Fig. 8). This is the case for species 1. Even though the direct effect of the environmental change is to increase the population growth rate of species 1 ($a_1 = 0.15$), strong indirect interactions with other species rotate the axis of orientation ($\cos\alpha_j$, $\cos\beta_j > 0$) so \mathbf{A} and \mathbf{B}_j lie on the same side of the surface defined by \mathbf{B}_i ($i \neq j$). Examining the regression coefficients, this results from a combination of direct competition with species 2 and "apparent" competition (Holt 1977, Abrams 1987) with species 2 through the shared predator species 4. The magnitudes of the change in mean population density of species 1 and 2 are similar, although for different reasons. Species 2 experiences relatively strong density-dependent buffering against changes in mean density ($\|\mathbf{B}_2\| \cos\beta_2 = 0.27$ vs. $\|\mathbf{B}_1\| \cos\beta_1 = 0.10$), although it suffers a relatively greater impact of the environment change ($\|\mathbf{A}\| \cos\alpha_2 = -0.22$ vs. $\|\mathbf{A}\| \cos$

$\alpha_1 = 0.083$). Finally, species 3 and 4 are relatively strongly buffered against change in mean population density due to density dependence ($\|\mathbf{B}_3\| \cos\beta_3 = 0.41$, $\|\mathbf{B}_4\| \cos\beta_4 = 0.22$).

To summarize the overall pattern exhibited by the four species, one can ask how important is $\|\mathbf{A}\| \cos\alpha_j$ relative to $\|\mathbf{B}_j\| \cos\beta_j$ in explaining the different magnitudes of response of species to the change in the mean of $u(t)$. From Eq. 10, $\log(\|\Delta N_j\|) = \log(\|\Delta U\|) + \log(\|\mathbf{A}\| \cos\alpha_j) - \log(\|\mathbf{B}_j\| \cos\beta_j)$, and taking the variance of both sides of this equality, $V[\log(\|\Delta N_j\|)] = V[\log(\|\mathbf{A}\| \cos\alpha_j)] + V[\log(\|\mathbf{B}_j\| \cos\beta_j)] - \text{COV}[\log(\|\mathbf{A}\| \cos\alpha_j), \log(\|\mathbf{B}_j\| \cos\beta_j)]$. For the four species in the simulation, $V[\log(\|\mathbf{A}\| \cos\alpha_j)] = 0.10$, $V[\log(\|\mathbf{B}_j\| \cos\beta_j)] = 0.35$, and $\text{COV}[\log(\|\mathbf{A}\| \cos\alpha_j), \log(\|\mathbf{B}_j\| \cos\beta_j)] = -0.12$. Therefore, variation in $\|\mathbf{B}_j\| \cos\beta_j$ explains roughly three times more of the variance in $\log(\|\Delta N_j\|)$ than variation in $\|\mathbf{A}\| \cos\alpha_j$. In other words, differences in density dependence experienced by different species are more important than differences in the effect of the environment on population growth rates when explaining the magnitude of response of different species to changes in the mean of $u(t)$.

Compensatory responses in mean densities

From Eq. 10, species that are similar to each other will likely show large changes in mean population density following an environmental change, because the buffering effect of density dependence $\|\mathbf{B}_j\| \cos\beta_j$ for each species will be weak. The question addressed here is whether the change in mean density of species i is opposite from the change in mean density of a similar species j . In other words, are changes in mean densities of similar species compensatory (Frost et al. 1994)?

To measure density compensation between two species, let

$$\chi_{ij} = \frac{(\Delta N_i + \Delta N_j)^2}{\Delta N_i^2 + \Delta N_j^2} - 1. \quad (11)$$

The numerator is the square of the expected change in the sum $N_i + N_j$, and the denominator is the sum of the squared expected changes in densities of each separate species. If complete compensation occurs, then $\Delta N_i = -\Delta N_j$, and $\chi_{ij} = -1$. On the other hand, if changes in mean densities are complementary, then $\Delta N_i = \Delta N_j$, and $\chi_{ij} = 1$. Values of χ_{ij} between -1 and 1 give the full range from compensation to complementation.

To derive an expression for χ_{ij} in terms of interactions among species, first define ϕ_{ij} as the angle between \mathbf{B}_i and the vector orthogonal to the vectors \mathbf{B}_k ($k \neq i, j$) and \mathbf{A} . The angles $\phi_{1,2}$ and $\phi_{2,1}$ are depicted in Fig. 9. Define θ_{ij} as the difference between ϕ_{ij} and $\phi_{j,i}$, and define γ_{ij} as the average of ϕ_{ij} and $\phi_{j,i}$; $\gamma_{ij} = (\phi_{ij} + \phi_{j,i})/2$. Heuristically, θ_{ij} measures the similarity between \mathbf{B}_i and \mathbf{B}_j relative to the vector orthogonal to the vectors \mathbf{B}_k ($k \neq i, j$) and \mathbf{A} , while γ_{ij} measures the similarity between the pair of species and the other

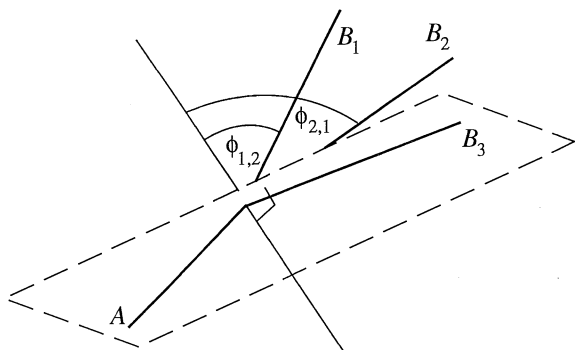


FIG. 9. Diagram giving a graphical interpretation of angles $\phi_{1,2}$ and $\phi_{2,1}$, which are the angles between B_1 and B_2 and the vector orthogonal to the surface spanned by B_3 and A .

species in the community. With these definitions (Appendix)

$$\chi_{i,j} = \frac{-2\|B_i\|\|B_j\|\cos(\gamma_{i,j} + \theta_{i,j}/2)\cos(\gamma_{i,j} - \theta_{i,j}/2)}{\|B_i\|^2\cos^2(\gamma_{i,j} + \theta_{i,j}/2) + \|B_j\|^2\cos^2(\gamma_{i,j} - \theta_{i,j}/2)} \quad (12)$$

Fig. 10 shows $\chi_{i,j}$ for different values of $\gamma_{i,j}$ and $\theta_{i,j}$ when $\|B_i\| = \|B_j\|$. Compensation is greatest for a pair of species when they are similar to each other ($\theta_{i,j}$ small), but different from the other species in the community, and different from the effects of the environmental stressor $u(t)$ ($\gamma_{i,j}$ small).

This result can be explained in biological terms. The greater the similarity between two species in terms of interactions with other species, the more a decrease in density of one species will be balanced by an increase in density of the other. This is because, with the reduction of one species, the other can fill its ecological position in the community. Furthermore, compensation increases with the differences between the pair of species and the other species in the community. If the two species are considered as an aggregate single species, then the greater their difference from the remaining species, the greater the buffering of their combined density against changes in the environmental mean. This in turn implies greater compensation between the species in order for there to be little change in the sum of their densities. The final component is the pattern of effects exerted by the environmental stressor. If A is similar to B_i and B_j , then the environmental effects on species i and j will be greater than those for other species. Therefore, they will both respond similarly to the environmental stressor, and this will decrease compensation.

Table 4 gives values of $\theta_{i,j}$, $\gamma_{i,j}$, and $\chi_{i,j}$ for each of the pairs of species in the simulated data from Eq. 7. As measured by $\theta_{i,j}$, the pair of species (1, 2) are the most similar ($\theta_{1,2} = -2.9$), which leads to strong compensation ($\chi_{1,2} = -0.97$). As measured by $\gamma_{i,j}$, the average effects of the species pair (2, 4) is very similar to the combined effects of the environment and other

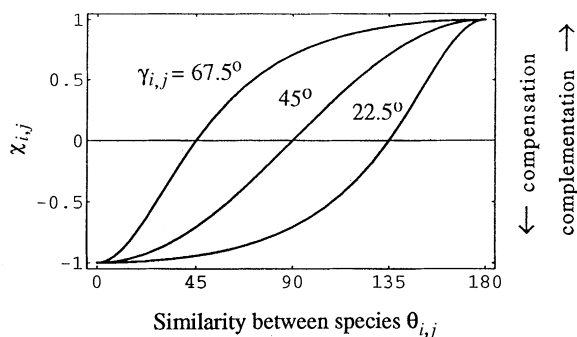


FIG. 10. The degree of compensation $\chi_{i,j}$ (Eq. 12) as a function of the angle $\theta_{i,j}$ for different values of $\gamma_{i,j}$. $\theta_{i,j}$ measures the difference between B_i and B_j orthogonal to the surface defined by the remaining values of B_k and A . $\gamma_{i,j}$ measures the difference between the sum of B_i and B_j , and the vector orthogonal to remaining values of B_k and A . The magnitudes of B_i and B_j , $\|B_i\|$ and $\|B_j\|$, are equal. The shape of Eq. 12 depends on the relative magnitudes of B_i and B_j , although the general shape is similar to that depicted in the figure.

species in the community ($\gamma_{2,4} = 89.5$) which leads to strong complementation ($\chi_{2,4} = 0.97$). Note that for the species pair (2, 4) the very strong complementation results from a value of $\gamma_{2,4}$ close to 90° rather than from a value of $\theta_{2,4}$ close to 180° (Fig. 10). Thus, even though species 2 and 4 are not particularly dissimilar from each other ($\theta_{2,4} = -29$), they still show strong complementation due to their pattern of interaction with the environment and other species in the community.

DISCUSSION

This paper has developed methods to predict the long-term changes in population densities that result from changes in an environmental stressor. The predictions are made using data on the short-term fluctuations in population densities driven by short-term environmental variability. The distinction between short- and long-term fluctuations in population densities is critical. Short-term population fluctuations reflect direct effects of environmental variability and interactions among species on population growth rates. In contrast, long-term changes in population densities may depend strongly on the indirect effects of interactions within and among species in a community. This distinction between short- and long-term changes in

TABLE 4. Measurement of compensation for the simulated data from Eq. 7.

Sp. i	Sp. j	$\theta_{i,j}$	$\gamma_{i,j}$	$\chi_{i,j}$
1	2	-2.9	75	-0.97
1	3	37	85	0.62
1	4	-9.4	56	-0.89
2	3	46	37	-0.74
2	4	-29	89.5	0.97
3	4	-13	72	-0.86

population densities is highlighted in Figs. 3 and 7, in which long-term changes in mean population densities in response to an environmental shift are much different than those observed at a shorter time scale.

To characterize interactions among species, the techniques developed here employ linear regression. The philosophy behind this approach is that linear regression gives the most powerful and easily applied statistical technique for examining interactions among species. An alternative approach might be to design a system-specific, detail-rich model for a given community and then analyze how the model responds to changes in an environmental stress parameter. Although there are clear advantages to this system-specific approach, it is limited by the amount of data needed to properly characterize a system and estimate model parameters. Nonlinearities in species interactions are notoriously difficult to characterize from data (Morris 1990, Carpenter et al. 1994). In the simulated multi-species example analyzed here, the linear regression approach gives better predictions than those from a nonlinear regression model, even though the nonlinear model has the same structure as the simulation model used to produce the data. This suggests that trying to incorporate nonlinearities may only muddy the predictions, because nonlinear models are more difficult to fit statistically than linear models. Of course, it is impossible to claim any generality from a single example, and more sophisticated methods than the ones I used for fitting nonlinear models may be more successful. However, this serves as an illustration that trying to incorporate nonlinearities is not essential to make predictions about changes in mean population densities.

In addition to quantitative predictions of long-term changes in population densities, the formulae derived throughout the paper give heuristic explanations for expected responses to environmental trends. When there are changes in the mean of an environmental stressor that affects population growth rates, the response of the mean population density of a species depends on the strength of the density-dependent interactions it exerts on itself and other species in the community; the greater the impact of a species on the population growth rates of other species in the community, the more that species is buffered against changes in the environmental mean (Eq. 10). The buffering effect of species interactions depends not only on the strength of interactions, but also on the pattern of interactions that defines the ecological functional role of a species in a community. Species that have unique ecological functions experience strong negative feedbacks against changes in their mean density. Together, these imply that "important" species in a community—those that interact strongly with other species and perform a unique ecological function—are the most strongly buffered by community interactions. A corollary of this result has practical application in conservation biology and ecological management. In

searching for indicator species that are sensitive to environmental disturbances, unique and strongly interacting species might make poor candidates due to the buffering effect of species interactions. This is not a hard and fast rule, since equally important is the sensitivity of population growth rates to the environmental stressor. However, all else being equal, functionally redundant species might make the best indicators of environmental change. This hypothesis is also derived by Carpenter et al. (1993) based on experimental manipulations of lake ecosystems; good indicator species are likely to be those whose ecological roles can be substituted by other species in the community.

When subject to an environmental trend, the mean densities of all interacting species in a community will shift in a complex pattern determined by the sensitivity of all species to the environmental stressor and the indirect effects of species interactions. To disentangle the complex community responses to environmental change, the community can be broken down into clusters of species having roughly the same ecological function. Within a cluster, changes in mean densities of species relative to each other will likely be large, while changes in the average mean density of species in the cluster relative to other clusters in the community will likely be small. This pattern is shown formally for clusters consisting of pairs of species in Eq. 12. (The analysis can be extended to larger clusters, although the requisite profusion of terms characterizing the similarity among species within and among the clusters makes the analysis cumbersome.) This result adds theoretical support to the relationship between the functional redundancy of species in a community and density compensation when subject to environmental change (Vitousek 1990, Frost et al. 1994).

This paper is aimed at predicting long-term changes in population densities, and all of the results are derived in terms of stationary population distributions. Critical issues that have not been addressed are how long it takes populations to reach the stationary population distribution, and how much data are needed to test the predictions with sufficient statistical power. Answers to these questions will depend strongly on the number of species in the community, the type of interactions among species, the amount of variability in population densities and the environment before an environmental change, and the quality of the data. Before applying the techniques to a particular data set, it would be wisest to construct a simulation model that mimics the dynamics of the system and test the techniques on the simulated data. Although the techniques worked well for the simulation models used here, I suspect they will fail when confronted with short data sets for many species that do not exhibit enough inherent variability to estimate regression coefficients accurately.

Despite the potential for complex positive and negative feedbacks driven by interactions within and among species, this paper provides simple qualitative

and quantitative predictions for how long-term environmental changes will affect population densities. The predictions are simple enough that they should be testable in a number of ecological systems. The main difficulty in predicting the consequences of environmental changes is the need to know the rudiments of how ecological systems work in the first place. Since we know little about the details of how ecological systems work, it seems reasonable to base predictions on the simplest possible information that can be extracted from data. This is the tack I have taken here.

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LITERATURE CITED

- Abrams, P. 1987. Indirect interactions between species that share a predator: varieties of indirect effects. Pages 38–54 in W. C. Kerfoot and A. Sih, editors. *Predation*. University Press of New England, Hanover, New Hampshire, USA.
- Apostol, T. M. 1969. *Calculus*. Volume 2. Blaisdell, Waltham, Massachusetts, USA.
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* **65**:1–13.
- Carpenter, S. R., K. L. Cottingham, and C. A. Stow. 1994. Fitting models for ecological interactions to time series with observation errors. *Ecology* **75**:1254–1264.
- Carpenter, S. R., T. M. Frost, J. F. Kitchell, and T. K. Kratz. 1993. Species dynamics and global environmental change: a perspective from ecosystem experiments. Pages 267–279 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. *Biotic interactions and global change*. Sinauer, Sunderland, Massachusetts, USA.
- Charles, D. F. 1991. *Acidic deposition and aquatic ecosystems: the barnacle case studies*. Springer-Verlag, New York, New York, USA.
- Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* **31**:61–104.
- Davidson, D. W., R. S. Inouye, and J. H. Brown. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology* **65**:1780–1786.
- Frost, T. M., S. R. Carpenter, A. R. Ives, and T. K. Kratz. 1994. Species compensation and complementation of ecosystem function. In C. G. Jones and J. H. Lawton, editors. *Linking species and ecosystems*. Chapman and Hall, New York, New York, USA, *in press*.
- Graedel, T. E., and P. J. Crutzen. 1990. The changing atmosphere. Pages 13–24 in *Managing planet earth*. W. H. Freeman, New York, New York, USA.
- Harrison, G. W., and S. Fekete. 1980. Resistance of nutrient cycling systems to perturbations of the flow rates. *Ecological Modelling* **10**:227–241.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* **91**:385–398.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**:197–229.
- Ives, A. R. 1995. Measuring resilience in stochastic systems. *Ecological Monographs* **65**:217–233.
- Ives, A. R., and G. Gilchrist. 1993. Climate change and ecological interactions. Pages 120–146 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Kareiva, P., J. G. Kingsolver, and R. B. Huey. 1993. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Lane, P. A. 1986. Symmetry, change, perturbation, and observing mode in natural communities. *Ecology* **67**:223–239.
- Leigh, E. 1975. Population fluctuations and community structure. Pages 67–88 in W. H. van Dobben and R. H. Lowe-McConnell, editors. *Unifying concepts in ecology*. Junk, The Hague, The Netherlands.
- Levine, S. H. 1976. Competitive interactions in ecosystems. *American Naturalist* **110**:903–910.
- Levins, R. 1975. Evolution in communities near equilibrium. Pages 16–50 in M. Cody and J. Diamond, editors. *Ecology and evolution of communities*. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.
- May, R. M. 1973. Stability in randomly fluctuating versus deterministic environments. *American Naturalist* **107**:621–650.
- . 1974. *Stability and complexity in model ecosystems*. Second edition. Princeton University Press, Princeton, New Jersey, USA.
- . 1981. Models for single populations. Pages 5–29 in R. M. May, editor. *Theoretical ecology*. Sinauer, Sunderland, Massachusetts, USA.
- Morris, W. F. 1990. Problems in detecting chaotic behavior in natural populations by fitting simple discrete models. *Ecology* **71**:1849–1862.
- Murdoch, W. W. 1993. Individual-based models for predicting effects of global change. Pages 147–164 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Nisbet, R. M., and W. S. C. Gurney. 1982. *Modelling fluctuating populations*. John Wiley & Sons, Chichester, UK.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemala. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118**:240–261.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- . 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**:667–685.
- Pimm, S. L. 1982. *Food webs*. Chapman and Hall, London, UK.
- Puccia, C. J., and R. Levins. 1991. Qualitative modeling in ecology: loop analysis, signed digraphs, and time averaging. Pages 119–143 in P. A. Fishwick and P. A. Luker, editors. *Qualitative simulation modeling and analysis*. Springer-Verlag, New York, New York, USA.
- Roughgarden, J. 1975. A simple model for population dynamics in stochastic environments. *American Naturalist* **109**:713–736.
- Royama, T. 1981. Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. *Ecological Monographs* **54**:429–462.
- Schindler, D. W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Oikos* **57**:25–41.
- Schneider, S. H. 1993. Scenarios of global warming. Pages 9–23 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. *Evolutionary, population and community responses to global change*. Sinauer Associates, Sunderland, Massachusetts, USA.

- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Second edition. W. H. Freeman & Company, New York, New York, USA.
- Strong, D. R. 1986a. Density vagueness: abiding the variance in the demography of real populations. Pages 257–268 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper & Row, New York, New York, USA.
- . 1986b. Density-vague population change. *Trends in Ecology and Evolution* **1**:39–42.
- Turchin, P. 1990. Rarity of density dependence or population regulation with lags? *Nature* **344**:660–663.
- Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time series. *Ecology* **73**:289–305.
- Turelli, M. 1977. Random environmental and stochastic calculus. *Theoretical Population Biology* **12**:140–178.
- . 1978. A reexamination of stability in randomly varying versus deterministic environments with comments on the stochastic theory of limiting similarity. *Theoretical Population Biology* **13**:244–267.
- Turelli, M., and J. H. Gillespie. 1980. Conditions for the existence of stationary densities for some two-dimensional diffusion processes with applications in population biology. *Theoretical Population Biology* **17**:167–189.
- Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* **57**:7–13.
- Webster, K. E., T. M. Frost, C. J. Watras, W. A. Swenson, M. Gonzalez, and P. J. Garrison. 1992. Complex biological response to the experimental acidification of Little Rock Lake, Wisconsin, USA. *Environmental Pollution* **78**:73–78.
- Wilkinson, L. 1987. *SYSTAT: the system for statistics*. SYSTAT, Evanston, Illinois, USA.
- Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* **75**:151–165.
- Yodzis, P. 1989. *Introduction to theoretical ecology*. Harper & Row, New York, New York, USA.

APPENDIX

This appendix derives Eq. 12 giving the degree of compensation of two species subject to an environmental change.

For notational clarity, consider the change in densities of species 1 and 2. From Eq. 9, the sum of the changes in mean density of species 1 and 2 is

$$\begin{aligned} \Delta N_1 + \Delta N_2 \\ = -\Delta U \frac{\det(A, B_2, B_3, \dots, B_S) + \det(B_1, A, B_3, \dots, B_S)}{\det(B_1, B_2, B_3, \dots, B_S)}. \end{aligned} \quad (\text{A.1})$$

Noting that $\det(A, B_2, B_3, \dots, B_S) = -\det(B_2, A, B_3, \dots, B_S)$

$$\begin{aligned} \Delta N_1 + \Delta N_2 \\ = \Delta U \frac{(\|B_1\| \cos \phi_{1,2} - \|B_2\| \cos \phi_{2,1}) \det(\hat{A}, \hat{B}_2, \dots, \hat{B}_S)}{\det(B_1, B_2, B_3, \dots, B_S)}, \end{aligned} \quad (\text{A.2})$$

where \hat{B}_i denotes the vector of length $S-1$ formed by removing the first element in B_i (Apostol 1969). With the definition of $\chi_{1,2}$ in Eq. 11, Eq. A2 leads directly to Eq. 12.

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